# Extirpation and Recolonization of the Buckeye, Junonia coenia (Nymphalidae) Following the Northern California Freeze of December, 1990

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Abstract. The Buckeye, *Junonia coenia*, seems to have been eradicated from its northern California range east of the San Francisco Bay area by a severe freeze the fourth week of December 1990. Reinvasion of the Sacramento Valley began at the end of June and many areas had been reoccupied by the end of the 1991 season. Population growth was approximately exponential during the reoccupation, but at season's end numbers were estimated at only 10% of average. No colonization was observed in the montane Sierra Nevada.

#### Introduction

In 1972 Ehrlich et al. observed that "... we believe that extinctions of local populations may be relatively commonplace in most temperate butterfly species, if not in most temperate animal species. That they are not more commonly observed and reported may well be an artifact of misapprehensions about the size of evolutionary and population-dynamic units... as well as the difficulty of 'proving' that a population of small, vagile organisms is no longer maintaining itself in an area." Since that time, extinction processes affecting threatened or endangered species have become an important topic of concern in ecology and conservation biology. Such butterflies are typically monophagous, stenotopic, univoltine and philopatric (Arnold 1981, 1983). Extinctions of common, "weedy" species are rarely noted, although in theory they should be very common. The Buckeye, Junonia (or Precis) coenia Hbn. (Nymphalidae), is about as different from an endangered Lycaenid as a butterfly can be; it is oligophagous, eurytopic, multivoltine and dispersive or even migratory. Such a species may be thought of as having no "permanent" populations at all, only constantly dynamic local manifestations of a large-scale or even global "metapopulation" (Andrewartha and Birch 1954, Levins 1970). Buckeyes may breed in a given locality for only one generation before dispersing, or being forced to disperse by seasonal changes in the ruderal vegetation. The larger entity - the metapopulation - may, however, be very persistent. In lowland California J. coenia is regarded as ubiquitous, common, and weedy (Garth and Tilden 1986; Tilden and Smith 1986).

The droughty winter of 1989-90 allowed the Buckeye to overwinter successfully in many atypical localities, as evidenced by the flight of adults in late winter and early spring where this is a rare event. In the California Central Valley the regular pattern of seasonal population growth was advanced by 1-2 generations, depending on locality. By autumn 1990 populations were very large in most areas, and adults were still flying as late as early December at the Suisun Marsh. Within three weeks the coldest weather in several decades gripped California. Although it cannot be rigorously proven, this freezing episode seems to have destroyed all of the Buckeye metapopulation east of the East Bay hills. This paper presents the available data on both the disappearance of the Buckeye and its gradual recolonization-reoccupation of its inland range in 1991.

### **The Normal Situation**

Junonia coenia ranges throughout the Central Valley, San Francisco Bay Area, foothills of the Coast Ranges and northern California mountains, and western foothills of the Sierra Nevada. Southward it extends across the Transverse Ranges and is common in coastal Southern California, but scarce in the deserts. At higher elevations in the northern mountains and Sierra Nevada it is a sporadic visitor from midsummer through autumn. When it arrives early enough it may breed successfully at least up to 2000m, but is unrecorded as overwintering at such altitudes. On the Sierran east slope it is often collected as singletons on flowers of Rabbitbrush (*Chrysothamnus*, Comositae) along highways (e.g., 89 and 395) in autumn. In some years it descends the Truckee River drainage to Reno, NV but its occurrence east of the Sierran crest is always chancy and short-lived.

Beginning in 1972, a transect has been maintained across northcentral California parallel to Interstate Highway 80 for studies of butterfly phenology and faunsitics. At present there are 10 stations on the transect. The number and identity of butterfly species flying at each is recorded on a biweekly sampling schedule throughout the season. Stations on the transect have been monitored from 6 to 20 yr. In addition, butterfly phenology is monitored closely on the floor of the Sacramento Valley at a network of stations not on the transect. I am thus in a good position to detect anomalies — such as the disappearance of a common species over a wide area for several months. I have in addition presenceabsence data from more or less regular trips to the north end of the State.

The Buckeye has been present at all low-elevation (below 1000m) transect stations in all years of record. That, however, does not mean it is a continuous resident. Shapiro (1974, p. 120) stated that it "is restricted to bottomlands early in the season, but generally distributed by late vi. It is not certain that *P. coenia* overwinters in the (Sacramento) Valley at all. It is abundant in the foothill canyons 3-6 wk before it appears on the Valley floor."

This assessment has held up. The first *J. coenia* on the Valley floor are usually seen in III or IV and occur in riparian habitat. They may have followed the streams down from the hills and are always spotty and rare; the species is almost never common before mid to late V.

The first specimens seen in foothill canyons are very small and clay-

colored beneath. This phenotype is produced in autumn everywhere, but infrequently seen in the Central Valley in spring. Table 1 demonstrates the high variance in first-flight dates for low-elevation stations since 1982, as well as the pattern of early appearance in the foothills (represented by Gates Canyon) as compared to the Valley, with the Suisun Marsh usually latest of all. Gates Canyon is an E-W oriented Coast Range

Station:					
Year:	Suisun Marsh	Gates Canyon	W. Sacramento	N. Sacramento	Rancho Cordova
1982	18.IV - 6.XII	21.III - 11.XII	1st Valley record 22.V	scord 22.V	22.V - 31.X
1983	10.VII - 23.X	24.V - 2.XI	1st Valley record 22.V	scord 22.V	4.VI - 11.XI
1984	10.VI - 1.XII	20.111 - 7.XII	1st Valley record 26.111	cord 26.111	1.VIII - 19.XI
1985	9.VI - 3.XI	7.IV - 17.XI	1st Valley record 18.II	icord 18.11	14.IV - 2.XI
1986	10.V - 6.XII	19.IV - 13.XI	3.III - 12.XI	No data	17.IV - 12.XI
1987	31.V - 15.XI	18.IV - 7.X	1st Valley record 26.IV	cord 26.IV	3.VII - 7.XI
1988	23.VI - 24.X	20.II - >21.Xª	5.II - >20.Xª	2.IV - >17.Xª	19.II - 10.XII
1989	4.IV - 18.XI	20.II - 19.XI	7.V - 15.XI	7.V - XI.20	30.I - 16.XI
1990	9.IV - 5.XII	22.I - 9.XI	17.III - 22.XI	5.I - 30.XI	10.VI - 17.XI
1991	10.VIII - 15.XI	17.VIII - 24.XII⁵	31.VII - 20.XII⁰	29.VI - 23.XI	16.VIII - 24.XI

canyon and itself averages 2-4 wk later for the Buckeye than the nearby N-S oriented Cold Canyon, which is monitored in spring but not part of the transect.

The Buckeye does occasionally appear at Valley sites as early as I, especially in drought years. There is no year-to-year pattern of repeated overwinter survival at particular Valley sites. I interpret the picture presented in table 1 as follows: the Buckeye is eradicated from most Valley sites in "normal" winters; the probability of successful overwintering is enhanced in drought years, but even then it is a rare and stochastic event. The Valley is recolonized during spring, mostly from foothill populations but perhaps with some contributions from locally overwintered animals. The population grows rapidly and always peaks in September-October, coinciding with the flowering time of Coyotebrush (*Baccharis pilularis*, Compositae), a favorite nectar source, and then tails off rapidly in November. In most years two or three apparent "waves" of migrating Buckeyes are seen passing through Davis during the summer and fall. Their general direction is S to N or SW to NE, but their sources are unknown and they are rarely abundant.

Junonia is a tropical and subtropical genus. In the eastern United States the northern boundary of J. coenia fluctuates from year to year, apparently due to cold intolerance. Opler and Krizek (1984) summarize a vast literature thus; "The Buckeye ranges from southern Canada through most of the United States to northern Mexico. Throughout most of its range the species cannot survive the winter, and year-round populations occur only in the southern portions of its range. It can survive the winter on coastal dunes as far north as North Carolina." Clark (1932) reported some overwintering at Washington, D.C., but his spring individuals could just as easily be immigrants. No one has even alleged the existence of a southward migration in autumn in the northern 2/3 of the range. Presumably, then, all reproduction in the north is ultimately in vain.

Northern California is the northernmost area where J. coenia is considered a permanent resident. Dornfeld (1980) treated it only as an immigrant into southern Oregon. The events of 1990-91 can be viewed as a temporary shift downslope and southward of the average threshold for successful overwintering near the northern edge of the species range.

#### **The Catastrophe**

On December 16-17, 1990 a low-pressure system from the Gulf of Alaska moved SE into northern British Columbia and Alberta, trailing a cold front. This is a normal sequence of events, but the context in which it occurred was not. A block in the northern hemisphere atmospheric circulation had ponded up a huge mass of stagnant, cold high pressure in the Arctic, and it eventually had to break out of confinement. Blocking high pressure remained over the Atlantic Ocean. The 16-17.XII system set the stage for the escape; when on 19.XII a second system moved southward on the Pacific coast, the pressure pattern allowed the bottledup Arctic air to rush straight southward instead of being deflected to the SE east of the Sierra Nevada, as normally occurs. From the 21st through the 24th, air direct from the Yukon flowed down into the Central Valley on gusty NNE winds induced by a low-level jet stream. The wind eased on Christmas Day but picked up again on the 26th, blowing until the end of the month. This was the worst cold wave in California since 1932, and in some areas since 1913. The worst night was the 22nd, setting dozens of records up and down the State. In many localities this was the coldest night ever recorded. Sensible temperatures (wind-chill temperatures) frequently dropped below zero F (-17.8°C). Of 190 California weather stations reporting deviations from 30-yr monthly mean temperatures in December, 187 were negative and the average deviation was greater than -3°F. Examples of climatological data for this period appear in tables 2-4.

Economic consequences were severe, reflecting the impact of such unusual temperatures on exotic species. The entire citrus crop was lost, and many trees were killed or badly damaged. The severity of damage was exacerbated by the desiccating effects of the wind; on the 22nd midafternoon humidities were near 10% at many stations, and overnight rebounded only to 40%. Vegetable crops were damaged, and recentlyplanted fields required replanting. Damage to exotic ornamentals was much more extensive than in the shorter freeze of 1972. Among woody genera severely damaged were *Eucalyptus*, *Grevillea* and *Brachychiton* (all from Australia). All specimens of Canary Island Pine, *Pinus canariensis*, in the Davis-Sacramento and Chico areas lost most of their needles. They appeared dead, but nearly all recovered. Standing dead and damaged *Eucalyptus* in the East Bay hills contributed to the destructive wildfire of 20-21.X.1991.

### **The Aftermath: Transect Data**

Numbers of individual butterflies are not counted as part of the transect study; only presence/absence data are taken. However, when I realized that the Buckeye was absent at all stations, I resolved to count all individuals of that species until numbers approached normal and this became impractical. That point was never reached in 1991.

On 31.III I saw a single female at Willow Slough, Yolo County, 5 km N Davis, on the floor of the Sacramento Valley. That is a normal time and place for a first Valley record of the year, but it is very unusual for no Buckeyes to have been seen by then in the foothills, and such was the case. (In 1985 the Buckeye was seen in the Valley before the foothills.) This was the last individual seen for 90 days! On 29.VI I observed two males in riparian habitat in North Sacramento, Sacramento Co. — one worn, one much fresher. 32 days later I saw another male in West Sacramento, Yolo Co. None was seen at the Suisun Marsh until 10.VIII (1 male): at Rancho Cordova, Sacramento Co., until 16.VIII (1 male); and in the foothills at Gates Canyon until 17.VIII (also 1 male). The cluster of mid-VIII sightings seems not to be coincidental. Single females in

From	
Table 2. Daily T observations (in 'F) for the second half of December, 1990 for selected stations affected by the freeze.	Climatological Data California Vol 00 #12 NOAA Achovilla N C
aily T observations (in °F) for the second half of Decembe	1/0/ 00 #10 NOAA Achovi

		Clinia	cilitiatological Data, California,	al Dala	, Ualli		VOI. 30 # 12, NUAA, ASREVIIIE, N.C.	#12,1	VOAA,	Asnev	ille, N.						
DATE:		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
STATION:																	
Davis 2 mi SW	MAX:	50	51	53	50	47	43	33	37	41	48	48	53	55	49	50	48
	MIN:	35	32	29	31	24	21	18	16	17	20	22	23	23	27	28	25
Fairfield <sup>a</sup>	MAX:	48	54	56	47	46	44	37	39	42	50	50	52	54	51	51	48
	MIN	39	39	31	31	31	25	17	19	21	23	26	28	28	30	24	24
Sacramento (Airport)	MAX:	53	53	52	49	43	34	37	42	48	48	51	54	48	50	49	53
	MIN:	38	33	32	30	23	22	18	20	19	22	23	26	25	27	20	24
Vacaville <sup>b</sup>	MAX:	55	58	50	52	45	38	37	41	49	50	56	55	50	52	47	54
	MIN	36	33	32	37	17	25	40	18	23	23	26	27	25	28	28	25
Winters	MAX:	51	55	61	51	50	44	36	39	42	51	52	57	54	50	51	49
	MIN:	36	36	33	35	25	23	19	15	21	21	24	24	24	27	24	24
Woodland	MAX:	49	52	54	52	48	42	32	37	41	48	49	53	52	48	49	46
	MIN:	37	38	30	32	24	21	19	19	23	24	28	26	27	27	24	27
San Francisco Airport	MAX:	53	59	56	50	46	40	38	42	49	52	55	51	54	52	50	53
	MIN	44	40	40	40	34	28	27	28	29	31	35	35	40	35	33	32
Placervilled	MAX:	44	52	52	51	40	36	31	34	42	45	47	52	57	48	48	50
	NIN	30	27	28	32	19	16	13	15	19	20	22	28	26	24	23	25
Notes: <sup>a</sup> adjacent to Suisun	un Marsh.		<sup>b</sup> adjacent to Gates Canyon.	to Ga	tes Ca	nyon.	°adja	cent to	cadiacent to San Bruno Mountain, where some survival occurred	Bruno I	Mounta	ain, wh	ere so	me su	rvival o	courre	0

<sup>a</sup> adjacent to Suisun Marsh. <sup>b</sup> adjacent to Gates Canyon. <sup>c</sup>adjacent to San Bruno Mountain, where some survival occurred (R.L. Langston). <sup>d</sup> representative Sierran foothill site (360m).

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Table 3. Departure of mean temperature from 30-yr means and lowest temperature (°F) registered for selected stations affected by the freeze, December 1990. From *Climatological Data, California, Vol 90* #12, NOAA, Asheville, N.C.

STATION:	Departure From Mean T:	Lowest T Recorded:
Angwin (Pacific Union College)	N.A.	16 F
Healdsburg	-4.1	14
Napa State Hospital	-6.2	14
Santa Rosa	-2.9	18
Auburn	-4.3	17
Chico University Farm	N.A.	17
Clearlake, 4 mi SE	N.A.	6
Fairfield	-4.0	17
Placerville	-1.4	13
Sacramento (Airport)	-4.6	18
Sacramento (City)	-3.8	18
Vacaville	-3.1	17
Willows 6 mi W	-4.1	11
Winters	-3.7	15
Woodland	-3.9	19
Davis 2 mi SW	-4.9	16
Palo Alto	-5.7	20
Redwood City	-5.4	19
San Francisco Airport	-2.8	27
Santa Cruz	-4.0	19
Watsonville Water works	-5.8	12
Modesto	-2.3	19
Stockton Fire Station #4	-5.3	15
Turlock	N.A.	19

apparent migratory flight were seen in Davis on 19.VIII (WNW to ESE) and 25.VIII (S to N), and a male was seen on flowers on 6.IX. These were the first Buckeyes of the year in Davis — two to three months later than average.

Numbers continued to increase in late summer and early autumn (table 5) in approximately the usual seasonal pattern, but remained far below average for calendar date. Since counts are not normally done, I can only guess that numbers were only about 10% of "average" in the late summer. *Junonia coenia* is normally present in every flower garden in Davis in September and October. In 1991 I never saw one in my garden, and sightings were so few that all were carefully noted. Other observers report similar experiences (see below).

Not one Buckeye was seen above 1000m in all my 1991 field work, although I spent 81 days afield in the Sierra Nevada and another 35 elsewhere in the mountains. On 19.X one male and two females were observed flying up the South Yuba River canyon near Washington, Nevada Co., at ca. 900m. By then, successful breeding was out of the question, and butterfly activity had ended there by 16.XI. Table 4. Minimum temperature records for Sacramento, December 1878 through 1987 with comparison to 1990 minima. Degrees Fahrenheit. From NOAA Technical Memorandum NWS WR-65 (Revised). Compare December 9-15, 1932.

			r		
Date	Record Low, Year	Low, 1990	Date	Record Low, Year	Low, 1990
1	32, 1929	29	17	28, 1928	33
2	30, 1906	31	18	28, 1924	32
3	32, 1918	33	19	25, 1924	30
4	29, 1909	34	20	27, 1928	23
5	32, 1972	36	21	26, 1928	22
6	29, 1891	34	22	25, 1928	18
7	28, 1891	33	23	28, 1930	20
8	27, 1972	31	24	25, 1879	19
9	23, 1932	32	25	26, 1891	22
10	22, 1932	39	26	25, 1879	23
11	17, 1932	46	27	27, 1878	26
12	21, 1932	35	28	26, 1930	25
13	23, 1932	36	29	24, 1878	27
14	23, 1940	32	30	28, 1962	20
15	26, 1932	39	31	24, 1915	24
16	26, 1892	38			

### **The Aftermath: Data From Others**

In September I wrote to a number of northern and central California Lepidopterists soliciting Buckeye data. A total of 18 respondents contributed to the synthesis which follows. Their experiences range from extensive field tripping to observing their own gardens. Information was received covering most of the area from Trinity and Siskiyou Cos. on the N to Inyo and Stanislaus Cos. on the S. A selection of observations follows; it must be stressed that none of those responding had found normal or nearly normal numbers of Buckeyes, and several had seen none at all to that time.

- W. Swisher (Santa Rosa): Only 1 or 2 between I and VI; perhaps 20% of "normal" numbers by IX.
- J. Mori (Modesto): None until 9.X (7 observed that date; 4 of these apparently migrating S to N).
- W. Patterson (Sacramento): "In II-III, 1990 common along Middle Fork American River (Sierra foothills); none in 1991. One 1 mi E Pilot Hill, Eldorado Co., 12.V.91. One at Del Puerto Canyon, Stanislaus Co. (Inner Coast Range), 30.VIII.91." (A Buckeye at Del Puerto Canyon would not normally be noteworthy at any time of year —AMS.)
- L. Smith (Sacramento): None in Sacramento until one each, 7.IX and 13.IX.

and the second s				
RANCHO CORDOVA	SUISUN MARSH	GATES CANYON	NORTH SACRAMENTO	WEST SACRAMENTO
1.1 - 0	16.I - 0	20.1 - 0	19.1 - 0	17.I - 0
18.I - O	22.1 - 0	30.1 - 0	26.1 - 0	23.1 - 0
29.1 - 0	9.II - 0	12.II - 0	7.II - 0	28.1 - 0
10.II - 0	18.II - 0	17.II - 0	14.II - 0	6.II - 0
20.II - 0	6.III - 0	24.II - 0	23.II - 0	16.II - 0
13.III - 0	27.III - 0	14.III - 0	16.III - 0	25.II - 0
29.III - 0	2.IV - 0	28.III - 0	30.III - 0	8.III - 0
4.IV - 0	10.IV - 0	3.IV - 0	7.IV - 0	22.III - 0
14.IV - 0	28.IV - 0	13.IV - 0	21.IV - 0	30.111 - 0
5.V - 0	14.V - 0	28.IV - 0	5.V - 0	9.IV - 0
16.V - 0	25.V - 0	11.V - 0	16.V - 0	17.IV - 0
30.V - 0	4.VI - 0	25.V - 0	28.V - 0	5.V - 0
19.VI - 0	20.VI - 0	3.VI - 0	12.VI - 0	19.V - 0
1.VII - 0	6.VII - 0	20.VI - 0	29.VI - 2	30.V - 0
16.VII - 0	21.VII - 0	9.VII - 0	15.VII - 0	15.VI - 0
1.VIII - 0	10.VIII - 1	4.VIII - 0	1.VIII - 1	29.VI - 0
16.VIII - 1	23.VIII - 0	17.VIII - 1	16.VIII - 1	14.VII - 0
31.VIII - 0	28.VIII - 6	3.IX - 0	2.IX - 2	31.VII - 1
15.IX - 4	7.IX - 1	11.IX - 11	15.IX - 1	15.VIII - 2
28.IX - 1	16.IX - 4	25.IX - 20	27.IX - 3	27.VIII - 3
13.X - 8	30.IX - 15	18.X - 10	11.X - 0	10.IX - 8
27.X - 10	14.X - 35	4.XI - 25	27.X - 8	24.IX - 5
9.XI - 0	1.XI - 0	22.XI - 2	11.XI - 1	11.X - 4
24.XI - 2	15.XI - 2	11.XII - 0	23.XI - 1	23.X - 2
9.XII - 0	29.XI - 0	24.XII - 3ª	4.XII - 0	5.XI - 0
	12.XII - 0		20.XII - 0	23.XI - 1
	19.XII - 0			1.XII - 0
				20.XII - 5ª

Table 5. Individual counts of Buckeyes at low-altitude transect stations, 1991.

<sup>a</sup> Apparently new emergence, much later than average.

- C. Nice (Davis): One each in Davis 29.VII, 20.VIII; three in West Sacramento, Yolo Co., 18.IX (about 3.5 km N of my West Sacramento site — AMS).
- G. Kareofelas (Davis): In extensive travels in northern California, only 3 Buckeyes seen in 1991: 1 at Grindstone Overlook, Glenn Co. (Inner North Coast Range), 4.VIII; 1 at Suisun City, Solano Co., 17.IX; 1 5 km S Rio Linda, Sacramento, Co., 22.XI.
- S. North (Arcata): A month late on North Coast and in Trinity Co.
- J.R. Tucker (Redding): None in Trinity foothills Weaverville area in spring.
- D. Giuliani (teste O. Shields): Several seen migrating W to E, along ridge running N from summit of Mt. Tamalpais, Marin Co.,

0
2
0
0
3
5
2
8
4
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0ª
8
6
0

Table 6. Biweekly total sightings of individual Buckeyes along the transect, 1991.

<sup>a</sup> Cold wave 22.X and heavy rain 25-26.X depressed counts.

19.X; several more also migrating W to E, Point Reyes Peninsula, 20.X.

Very detailed data were received from two respondents, viz.:

- O. Shields (Mariposa): None seen in Mariposa Co. until mid-IX. At Jerseydale, Mariposa Co., 1 ♀ 12.IX, 1 ♂ 23.IX, 1 ♀ 1.X, 2 ♀ 4.X, then continuously present until 2.XI, commonest in mid-X when up to 15 were counted on 16.X, with some evidence of migratory movement toward the SW 16-24.X. Also 2 seen at Mariposa, 7.XI. Also 2 seen in Monterey Co., 8.IX.
- R. Langston (Kensington): "Buckeyes are usually observed in small numbers November through February in most winters in the Bay Area." He provides winter counts at San Bruno Mountain for 1989-90 and 1990-91. The last specimen seen in 1990 was on 28.XI: zero seen in 12 days in XII, zero in 16 days in I.91; the first post-freeze sighting was on 15.III and numbers in IV were low. "By mid-IX the Buckeye in 'fair' numbers on SBM and noted in Kensington. However, quite scarce on 3 Xerces (Fourth of July) counts where usually much commoner:...Berkeley (15), Mt. Diablo (4), and South San Francisco Bay (only 1!)."

## Discussion

This level of coverage is far spottier than one would have arranged had there been advance warning. Still, it is good enough to persuade one that *Junonia coenia* experienced a severe die-off during the December 1990

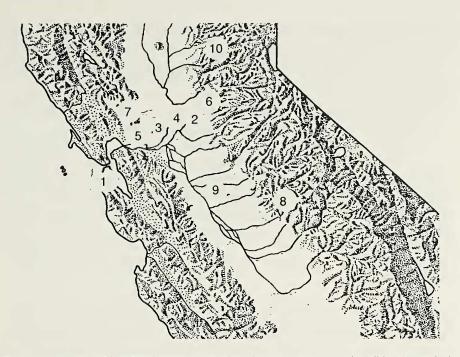


Fig. 1. Sequence of first Buckeye observations in 1991 at transect localities (sampled biweekly) and localities with a resident observer.

Localities:

- 1 San Bruno Mountain 15.III
- 2 North Sacramento 29.VI
- 3 Davis 29.VII
- 4 West Sacramento 31.VII
- 5 Suisun Marsh 10.VIII
- 6 Rancho Cordova 16.VII
- 7 Gates Canyon 17.VIII
- 8 Jerseydale 12.IX
- 9 Modesto 9.X
- 10 Washington 19.X

freeze and gradually reoccupied much of the lost territory during the second half of summer 1991. The meteorological records indicate that the freeze was most severe inland, so it is not surprising that Buckeye survival seems to have been better at the coast (Langston and J.A. Powell). It is not, however, certain that recolonization of the Sacramento Valley proceeded from the Bay Area by way of the Sacramento-San Joaquin Delta, since recolonization of the Suisun Marsh was so late in comparison with metropolitan Sacramento. Mori reports no Buckeyes at Modesto until early October, the same time they became common in the Sierran foothills in Mariposa Co. (Shields). The apparent wave of immigrants observed at Davis in mid-August showed no clear-cut directionality. It may be that recolonization resulted from the spreading out of several independent foci where some overwinter survival had occurred, rather than being traceable to a single source. At any rate, the various local populations had effectively coalesced at least near Sacramento by

the end of the season, as normally happens several months earlier (fig. 1).

As far as I know, there are no quantitative data demonstrating that Buckeye population growth in normal Central Valley summers is an exponential process, but my subjective impression after 20 yr is that it is. When the total number of observations on the transect is summed for each biweekly sampling cycle, the result for 1991 is very nearly an exponential process, with a doubling time of nearly 3 wk during the interval late VI-early X (table 6). This can only be suggestive, but it does suggest that Buckeye populations grew in reasonably normal fashion in 1991 but with a substantial handicap due to their late start, which they could not overcome before the season came to an end. Just as an early start due to a dry, mild winter seems to have led to an outstanding Buckeye flight in 1990, the freeze of December 1990 set up the Buckeye with unusually low numbers of individuals attempting to hibernate over the winter of 1991-92.

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